# An Introgression Line Population of *Lycopersicon pennellii* in the Cultivated Tomato Enables the Identification and Fine Mapping of Yield-Associated QTL

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Manuscript received March 6, 1995
Accepted for publication August 11, 1995

ABSTRACT

Methodologies for mapping of genes underlying quantitative traits have advanced considerably but have not been accompanied by a parallel development of new population structures. We present a novel population consisting of 50 introgression lines (ILs) originating from a cross between the green-fruited species *Lycopersicon pennellii* and the cultivated tomato (cv M82). Each of the lines contains a single homozygous restriction fragment length polymorphism-defined *L. pennellii* chromosome segment, and together the lines provide complete coverage of the genome and a set of lines nearly isogenic to M82. A field trial of the ILs and their hybrids revealed at least 23 quantitative trait loci (QTL) for total soluble solids content and 18 for fruit mass; these estimates are twice as high as previously reported estimates based on traditional mapping populations. For finer mapping of a QTL affecting fruit mass, the introgressed segment was recombined into smaller fragments that allowed the identification of three linked loci. At least 16 QTL for plant weight, 22 for percentage green fruit weight, 11 for total yield and 14 for total soluble solids yield were identified. Gene action for fruit and plant characteristics was mainly additive, while overdominance (or pseudo-overdominance) of wild species introgressions was detected for yield.

COMPLETE linkage maps of DNA markers have facilitated mapping of genes affecting quantitatively inherited traits (PATERSON *et al.* 1991a; TANKSLEY 1993). Suitable mapping populations for such studies must possess sufficient polymorphism for marker analysis and for quantitative traits. For self-pollinated crops, such as rice (CAUSSE *et al.* 1994), soybean (KEIM *et al.* 1990) and tomato (MILLER and TANKSLEY 1990), little variation between cultivated varieties is detectable by DNA markers. To overcome this problem, studies of quantitative trait loci (QTL) were performed on wide crosses between species or races. The population structures most commonly used for QTL mapping in self-pollinated crops were $F_2/F_3$ or recombinant inbreds.

Conventional mapping populations have several limitations in the accurate identification and fine mapping of QTL. One of the major shortcomings is their resolution power. In a simulation study on backcross populations, it was demonstrated that for QTL of large effects, in experiments with large populations and high density linkage maps, the confidence interval for QTL map location is on the order of 10 cM (DARVASI *et al.* 1993). Another limitation is in the ability to identify QTL with small effects. In many instances it was found that a large portion of the phenotypic variation for the measured traits could be explained by the segregation of a few major QTL. For example, 33–37% of the phenotypic variation for seed weight in cowpea and mungbean was explained by a single QTL (FATOKUN *et al.* 1992). A QTL for glume hardness explained 42% of the variation in a maize-teosinte cross (DOEBLEY and STEC 1991). A major QTL can overshadow the effects of minor independently segregating QTL by increasing the total phenotypic variation, and thus genes with lesser effects might fall below the threshold of detection. The overshadowing effect interferes with the correct estimation of the number of QTL and with their fine mapping. An additional restriction of standard populations may result from the interaction between two unlinked QTL. Interacting loci can reduce the difference between the subgroups of the tested QTL and therefore the loci may escape detection.

In tomato, which has been a model plant for QTL mapping, the low level of variation among the cultivated varieties is not limited to RFLPs but is also typical of agronomically important traits. The narrow genetic basis of the cultivated tomato has emphasized the value of exotic germplasm for improvement of the crop (RICK 1982). QTL studies with complete genome coverage in tomato have been conducted on backcross (PATERSON *et al.* 1988), $F_2/F_3$ (PATERSON *et al.* 1991b) and recombinant inbred populations (GOLDMAN *et al.* 1995) involving interspecific crosses. In these populations each of the segregating plants possessed a large fraction of the wild species genome and some individuals were characterized by partial or complete sterility. A few major

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genes for sterility can exert an overshadowing effect on QTL that might be of great interest. For this reason it has not been possible to map QTL for increased yield in tomato, and studies have focused instead on fruit characteristics, abiotic stress tolerance, insect resistance or morphological variation of the young seedlings (NIENHUIS *et al.* 1987; PATERSON *et al.* 1988; MARTIN *et al.* 1989; DE VICENTE and TANKSLEY 1993).

To overcome the problem of interspecific mapping of QTL associated with yield, we modified population structures used in the past by combining them with DNA markers. WEHRHAHN and ALLARD (1965) have demonstrated that effects of individual QTL in wheat can be measured by using backcross inbred lines (BILs). BILs are characterized by the low proportion of the donor parent in each of the population members and therefore are ideally suited for mapping interspecific variation.

In this paper we describe the application of a novel introgression line (IL) population, which resembles the BILs, for the mapping of interspecific variation for quantitative traits associated with yield in tomato. The IL population is comprised of 50 *L. esculentum* lines, each containing a single homozygous restriction fragment length polymorphism (RFLP)-defined chromosome segment, introduced from the green-fruited species *L. pennellii* (ESHED and ZAMIR 1994b). Among the lines there is a complete representation of the wild species genome. The ILs are nearly isogenic to the recipient genotype, and therefore all the genetic variation that differentiate them can be associated with the introgressed segment. Since each line carries only a small fraction of the wild species genome, most of the fertility problems can be eliminated and yield-associated traits can be measured. We demonstrate that the alternative mapping population structure presented here could increase the ability of geneticists to dissect a quantitative trait by using saturated RFLP linkage maps.

## MATERIALS AND METHODS

**Plant material:** The parental lines for the IL population were the processing tomato inbred variety M82 (*L. esculentum*) and the inbred accession of *L. pennellii* (LA 716). The development scheme of the ILs, through repeated backcrossing and RFLP selection, was described previously by ESHED and ZAMIR (1994b). The IL population is composed of 50 *L. esculentum* ($x = 12$) lines, each containing a single RFLP-defined chromosome segment of *L. pennellii* (Figure 1). The lines contain an average of 33 cM from a total genome size of 1200 cM (2.75%); overlapping regions between neighboring lines were selected to ensure complete representation of the wild species genome. The total length of the overlaps is 480 cM. Determination of the size and identity of introgressed segments was based on RFLP analysis of 375 markers chosen to cover the entire tomato genetic map at minimal intervals. Our claim that the lines contain a single introgression is based on the RFLP analysis, which in no case revealed additional independent introgressions. The purity of the ILs is also supported by fingerprinting of the lines with multicopy microsatellite probes (ESHED and ZAMIR, unpublished data). It should be noted that the introgression of IL8-1 was the only one that was not assayed in homozygous condition; this was because of elimination of male gametes carrying the *L. pennellii* allele (ESHED and ZAMIR, unpublished data).

For the analysis described in this study, the 50 ILs were both selfed and crossed with M82 and A8 (a different processing inbred with larger fruit and higher content of soluble solids) (Table 1). The following genotypes were transplanted in the field in Akko on March 1993 in a completely randomized design: *L. pennellii* (eight plants), M82 (30 plants), A8 (23 plants), hybrids of A8 with M82 (20 plants), $F_1$-interspecific hybrids (20 plants), selfed progenies of each of the 49 homozygous ILs (six plants), hybrids of ILs with M82 (six plants each) and hybrids of ILs with A8 (six plants each). Hybrids heterozygous for the introgression IL8-1 were selected using the isozyme marker *Aps-2*. Seedlings (35 days old) were transplanted into a drip-irrigated field with 50 cm between plants and 2 m between rows (1 $m^2$ per plant).

Two regions of the genome were selected for the fine mapping analysis in 1994. One region was covered by IL2-5 and IL2-6 and was associated with small fruit size. The other was contained in IL1-4 and was associated with high yield of total soluble solids (BY). Large $F_2$s of a cross between these ILs with M82 were grown, and recombinants in the targeted regions were selected following RFLP analysis (BERNATZKY and TANKSLEY 1986) with the most distal markers defining the introgressions. Recombinant plants were subjected to RFLP analysis with additional markers available for the introgressed segments to define their genotype. Recombinants of interest were selfed again to obtain lines homozygous for shorter introgressions. After lines for the fine mapping analysis were fixed in a homozygous condition, their progeny were transplanted in the field in Akko on March 1994 (10 plants from each IL and 30 plants from M82 in a completely randomized design). For fruit mass mapping only selfed plants were grown, while for the BY analysis selfed progenies and hybrids with M82 were tested.

**Phenotyping:** Fruits of all lines were harvested when 95–100% of the tomatoes of M82 were red (105 days after transplanting in the field). The following measurements were taken for each of the plants: weight of the vegetative part (PW), percentage green fruit weight at harvest time (G), and red fruit weight. Total fresh yield per plant (Y) included both the red and green fruit. The experiment was harvested according to the order of the planting in the rows and not based on maturity level. Under field conditions toward harvest time, every day ~3% of the fruit change their color from green to red. Therefore it is reasonable to expect that even the late maturing genotypes would have reached complete maturity had the plants been harvested a few days later. For this reason our yield parameter for each of the genotypes included both the red and green fruit weight. Total soluble solids concentration – Brix (B) represents mainly the soluble sugars and acid concentration in the fruit and is a standard quality parameter for the processing tomato industry. B was assayed on a sample of 20 red fruits per plant (measured using the digital refractometer RFM-80 BS), and mean fruit mass (FM) was calculated from all the red fruits. The product of Y and B provides an estimate of the grams of soluble solids produced per plant (BY).

**Statistical analysis:** Statistical analyses were performed on the JMP V.3.1 software package for Macintosh (SAS Institute 1994). Mean values of the parameters measured for the tested genotypes were compared to the appropriate control genotypes using the "Fit *Y* by *X*" function and "Compare with control" with an alpha level of 0.05 (DUNNET 1955). M82 was the common control for the ILs and their hybrids with M82; M82 × A8 was the common control for the hybrids of the ILs with A8. The additive effect (*a*) was half of the difference

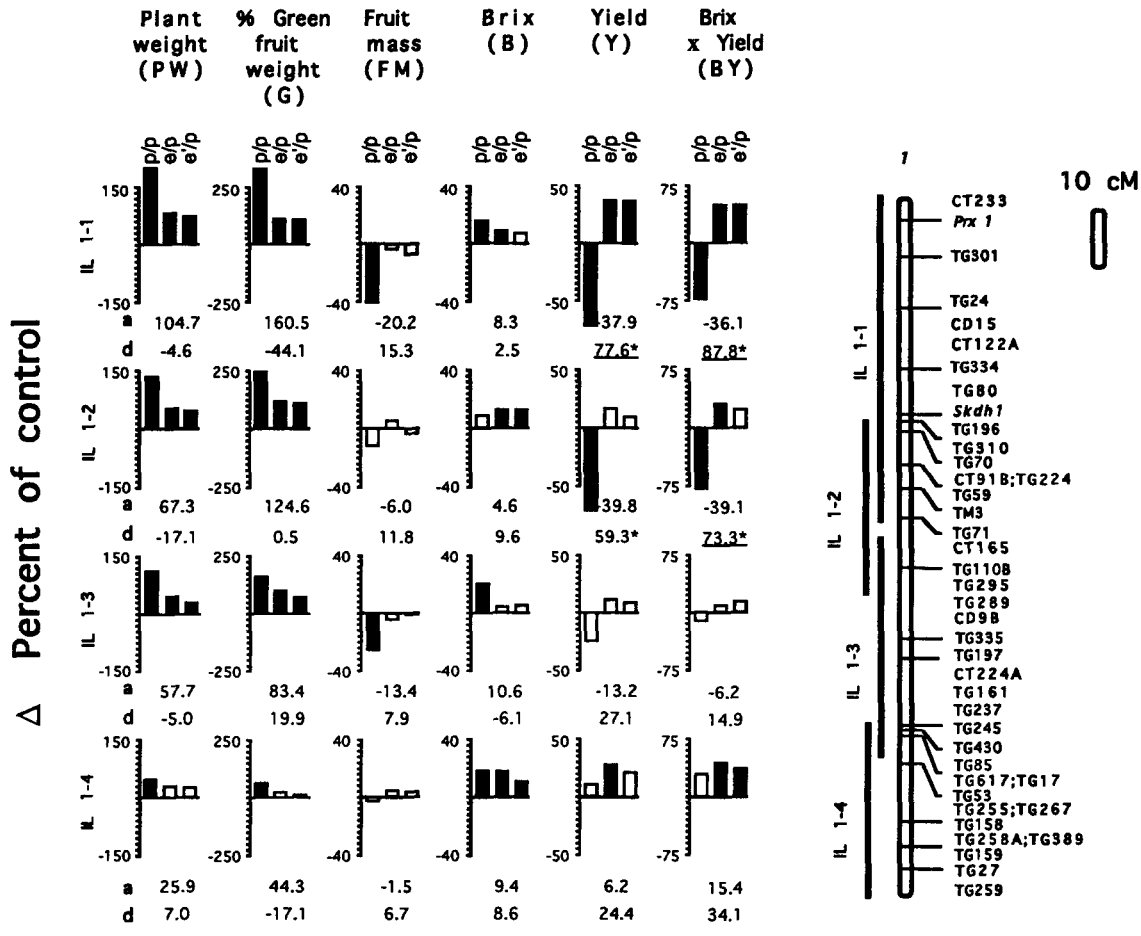


FIGURE 1.—The chromosomal location, size, identity and phenotypic effects of the 50 *L. pennellii* ILs. The genetic map was constructed on the basis of 119 BC1 plants as described by ESHED *et al.* (1992). Mapped markers are connected to the chromosome with a horizontal line, and markers not assayed on the BC1 map are placed according to their approximate positions according to TANKSLEY *et al.* (1992). Each line was probed with all the markers, and the ones showing the wild species alleles are marked by the bar to the left of the chromosome. The phenotypic difference (as percentage of control) for each of the ILs and their hybrids is given for the following traits: PW, plant weight; G, percentage green fruit at harvest time; FM, fruit mass; B, total soluble solids – Brix; Y, yield; BY, Brix × yield. For each trait the left bar represents the relative performance of the ILs (p/p), the central bar shows the effects of hybrids with M82 (e/p), and the bar at the right is the relative performance of the hybrid with the tester A8 (e'/p) (the control is M82 × A8). Bars in black indicate significant differences exceeding $p < 0.05$, and empty bars indicate nonsignificant differences. The following components of genetic variability for each IL × trait are presented as percentage of control (M82). The additive effect (a) is half of the difference between the IL and M82, and its significance was calculated on the basis of the comparison between them. The dominance deviation (*d*) is the difference between IL × M82 and the midvalue of its parents. Significant *d* values at the $p < 0.05$ are marked by *. Significant overdominance at the $p < 0.05$ level is marked by an underline of the *d* value.

between each IL and M82, and its significance level was determined by the comparison between the IL and M82. The dominance deviation (*d*) and its significance were calculated by contrasting the IL × M82 (+1) with M82 (−0.5) and the appropriate IL (−0.5). The threshhold level for significant *d* values was 0.001, which provides an experiment-wise error of 0.05 for the 50 compared genotypes. All calculations were performed with the measured values, except for G, where square root transformation was evaluated to improve normality. Results are presented as the percent difference (Δ%) from isogenic control. Interaction with genetic background (hybrids of ILs with M82 and with A8) was determined for each introgression by two way analysis of variance with significance threshhold of 0.001. The coefficient of variation (CV) for each trait was calculated by dividing the general (over all tested genotypes) SD by the general mean. The minimum number of $p < 0.05$ significant QTL affecting a trait (Table 2) was calculated on the basis of the following assumptions: 1) each IL affecting the trait carries only a single QTL, 2) two overlapping introgressions with a significant effect on the trait (in the same direction relative to the control) carry the same QTL and 3) a QTL is counted only if the IL or its hybrid is significantly different from the corresponding control, regardless of the significance of *a* and *d*. The mean degree of dominance for each trait (*d*/[*a*]) (Table 2) was calculated from the mean dominance deviation for all ILs divided by the mean additive effect.

For the 1994 trial, a multiple range test between the lines evaluated for the finer mapping of the introgression of interest was performed by the "Fit *Y* by *X*" function and "Each pair comparison" with an alpha level of 0.05. For comparisons of the lines derived from IL1-4, the inbred ILs and the hybrids of ILs × M82 were compared separately. M82 was included in both comparisons as a control.

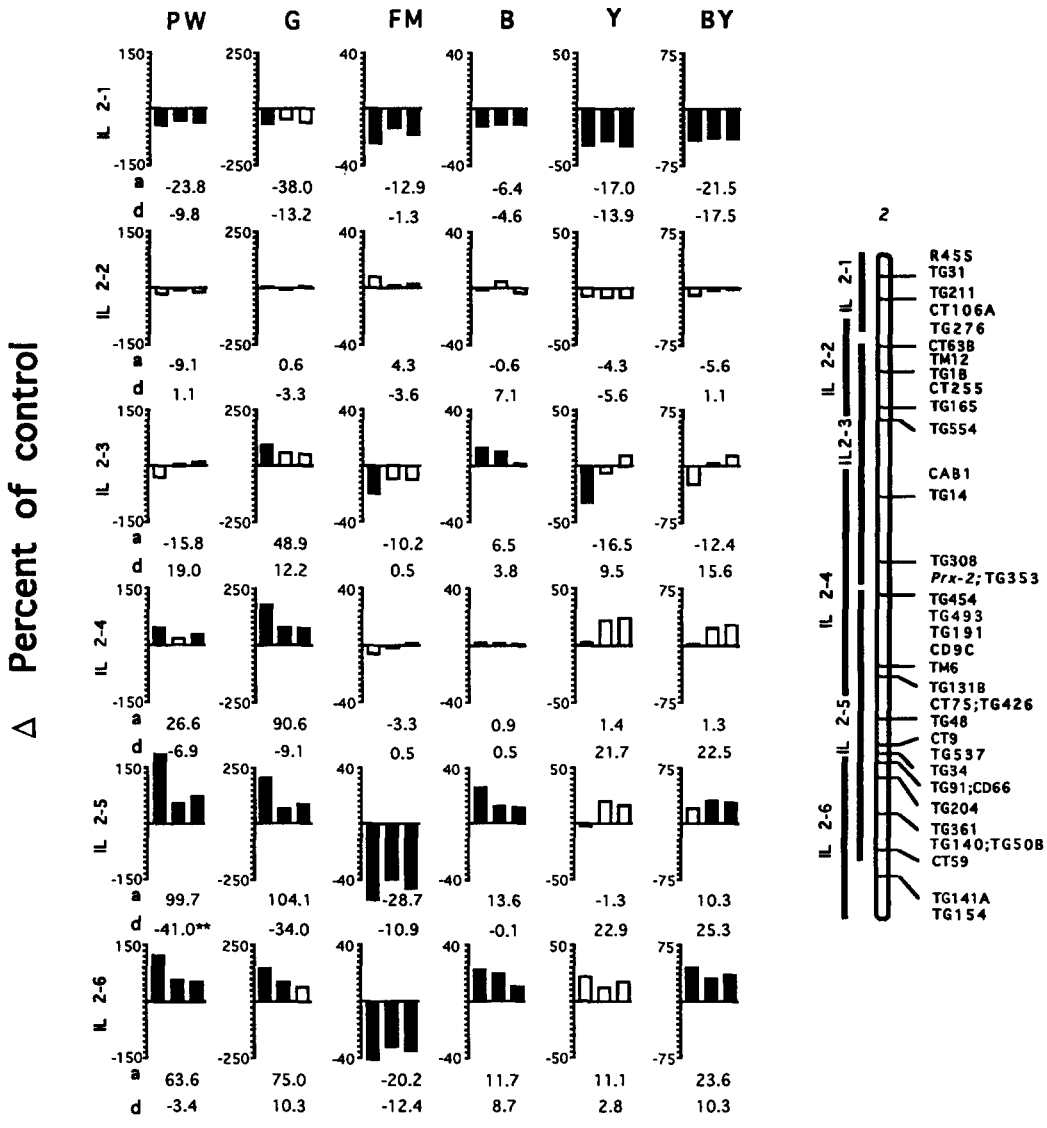


FIGURE 1.—*Continued*

## RESULTS

**Phenotype of parental species and their $F_1$ hybrid:** The parental species and their interspecific hybrid were characterized for the quantitative traits under investigation. Highly significant differences between *L. esculentum* and the $F_1$ hybrid were found for all measured traits except BY (Table 1). The vigor of the $F_1$ hybrid was most striking for PW, which was 24 times higher than for M82 and eight times higher than for *L. pennellii*.

*L. pennellii* did not set fruit under the field conditions where the Y of the hybrid was 50% of that of M82; this difference in fruit set could have affected PW, since there is competition for assimilates between the vegetative and the reproductive organs of the plant. To eliminate the effect of variation for fruit set from the study of vegetative growth, *L. pennellii* was compared in the following year to a male-sterile isoline of M82; their plant weights were very similar (8.8 and 7.1 kg per plant, respectively), while plant weight of their hybrid was seven times higher than that of the parents.

Another factor that might influence PW is growth habit: M82 is a determinate plant due to homozygosity for the recessive mutation *sp* (self-pruning), whereas *L. pennellii* and the $F_1$ are indeterminate. *L. pennellii* was also compared to an indeterminate male-sterile *L. esculentum* line (*Sp/Sp*) for evaluation of the effect of the mutation *sp* on plant growth. The sterile indeterminate line was more than twice as large as the sterile M82 or *L. pennellii*. PW (both fresh and dry) of the $F_1$ hybrid between the wild species and the indeterminate *L. esculentum* line was 3.7 times higher than that of the indeterminate sterile *L. esculentum* parent. This result indicates that only a part of the heterotic effect observed for growth rate of the vegetative parts can be attributed to the differences in fruit set ability and growth habit between the two species.

Large differences in FM, B and G between the two

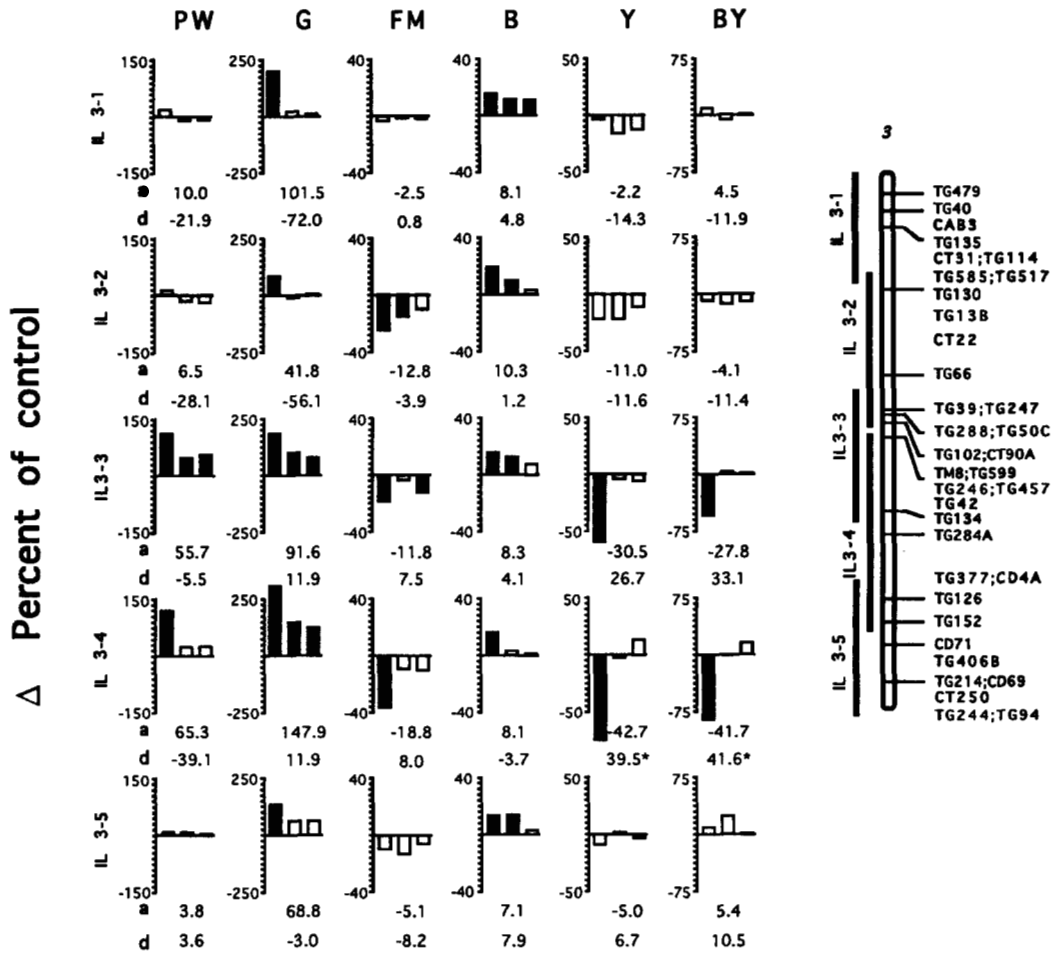


FIGURE 1.—*Continued*

parental species can be inferred from a comparison of *L. esculentum* with the interspecific $F_1$ hybrid. The wild species was responsible for lower FM, higher B and higher G (Table 1).

**Phenotypic analysis of the IL population:** The IL population did not appear markedly different from the cultivated varieties (Table 1). The plants of the ILs were bigger, with later ripening, lower fruit mass, higher soluble solids content (Brix) and lower yield than the control. When tested as hybrids, BY was higher than the controls, while for the other measured traits they were generally intermediate between the inbred ILs and the controls.

*Plant weight (PW):* Of the 49 ILs presented in Figure 1, 24 had a significantly different PW at harvest date compared to M82 (Table 2). IL1-1 had the highest PW in the experiment, *i.e.,* 209% higher than M82, while IL1-1 × M82 had a 100% increase relative to M82. In the A8 × M82 genetic background the same introgression had a very similar effect, contributing to a 91% increase in plant weight (Figure 1). IL1-1 and IL1-2 had very similar effects on plant weight as well as other traits discussed below, suggesting that these QTL reside in their overlapping segment. It is interesting to note that both lines carry the *S* (self-incompatibility) (LIEDL *et al.* 1993) locus, which in a homozygous state produces almost sterile plants of very strong vegetative growth. IL6-2 and IL6-3 are both of indeterminate growth habit due to the allele *Sp* originating from *L. pennellii;* however, PW of IL6-2 was 58% lower than that of the control, while PW of IL6-3 was 173% higher. Since PWs of the hybrids of both ILs were much higher than that of the control, we conclude that the difference between the two is due to homozygosity in IL6-2 for the recessive mutation *ndw* (necrotic dwarf) (WEIDE *et al.* 1993).

In 22 ILs there was a significant additive effect (*a*) associated with an increase of PW, whereas only two ILs were associated with a significant decrease in PW. The two indeterminate ILs (IL6-2 and IL6-3) had a significantly increased dominance deviation, of which one (IL6-2) was overdominant. Overall, PW showed additive inheritance ($d/[a] = 0.06$), and the minimal number of QTL affecting the trait was 16.

*Percentage green fruit weight (G):* Processing tomato varieties were developed for a single harvest that takes place when 95–100% of the fruits are mature red. Since the ILs were harvested together, G represents the relative earliness of the different genotypes. G in the ILs

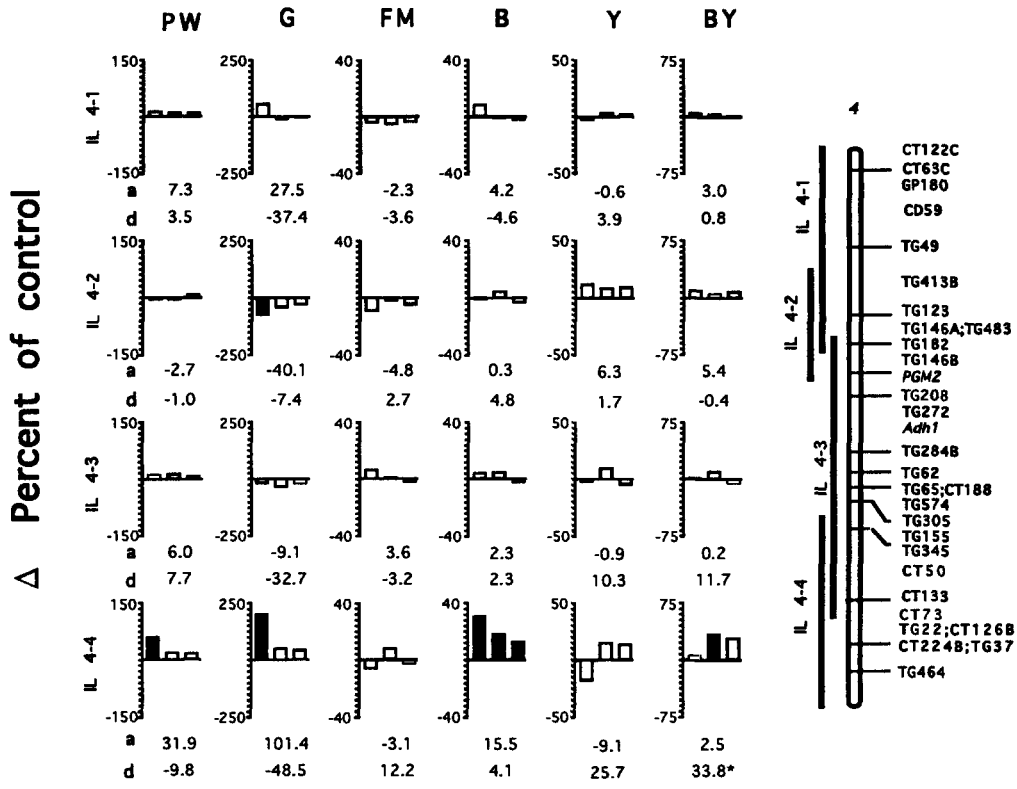


FIGURE 1.—*Continued*

showed a binomial distribution and therefore a square root transformation was performed. Significantly late ripening characterized 33 of the 49 ILs; only IL2-1 and IL4-2 ripened significantly earlier than the control. Two ILs (IL 6-2 and IL 7-2) showed a significant dominance deviation but none was overdominant. G was generally inherited in an additive manner and the minimum number of significant QTL was estimated as 22.

*Fruit mass (FM):* In 22 ILs, FM was lower than in the control. However, IL7-5 and IL12-1 contained genes originating from *L. pennellii,* which increased FM, indicating transgressive segregation. The smallest fruit size was measured in IL6-2 (homozygous for *ndw*); this was followed by IL2-5, which was subjected to fine mapping (discussed later). The *L. esculentum* alleles, generally producing higher FM, showed partial dominance over the *L. pennellii* alleles ($d/[a] = 0.34$). The minimum number of QTL estimated for this trait was 18.

*Total soluble solids concentration – Brix (B):* In 31 ILs the B values were significantly higher than in the control, and only IL2-1 had a lower B value than M82. The highest B values were found for IL6-2 and IL6-3, which were indeterminate. These two lines differ from M82 in their growth habit (indeterminate *vs.* determinate), and this is known to have a major effect on B (EMERY and MUNGER 1970). The minimum number of QTL affecting B was 23, with generally partial dominance to the *L. pennellii* alleles for higher B values.

*Total fruit yield (Y):* Nine homozygous ILs had significantly lower Y values than M82, while only IL7-5 had a higher Y. Unlike the previous traits, Y of the hybrids could not be predicted from the Y of their inbred IL parents. The ILs with the lowest Y values in a homozygous condition (IL1-1, IL1-2, IL3-3, IL3-4, IL6-2 and IL7-2) gave rise to hybrids with Y values equal or superior to those of controls. Seven ILs with significant dominance deviation for increased Y were identified. Three of these (IL1-1, IL5-4, and IL7-3) showed significant overdominance, indicating that the hybrid outyielded its highest parent. Hybrids of IL1-4, IL6-3, IL7-5 and IL9-2 had higher Y values than M82 but not from their homozygous IL parent. The minimum number of QTL for Y was 11, and the mode of inheritance was largely overdominant ($d/[a] = 2.16$).

*Total yield × Brix (BY):* In tomatoes there is a negative relationship between total fruit yield and soluble solids concentration (STEVENS and RUDICH 1978). Therefore, the parameter BY provides both a biological and an agricultural estimate for the productivity of the plant. To obtain a better estimate of QTL affecting the horticultural yield, we analyzed the derived product BY. This product gives an estimate for the g of soluble solids produced per plant. IL2-6, IL6-3, IL7-5, IL9-2 and IL11-2 had significantly higher BY than M82. All of these lines were also distinguished from M82 in having larger and later maturing plants so their advantage can be explained by the larger source and the longer time of assimilate production. The same was true for the hybrids of IL1-1, IL1-2, IL5-4, IL6-2 and IL7-3, all of which showed significant overdominance for this trait. IL2-1

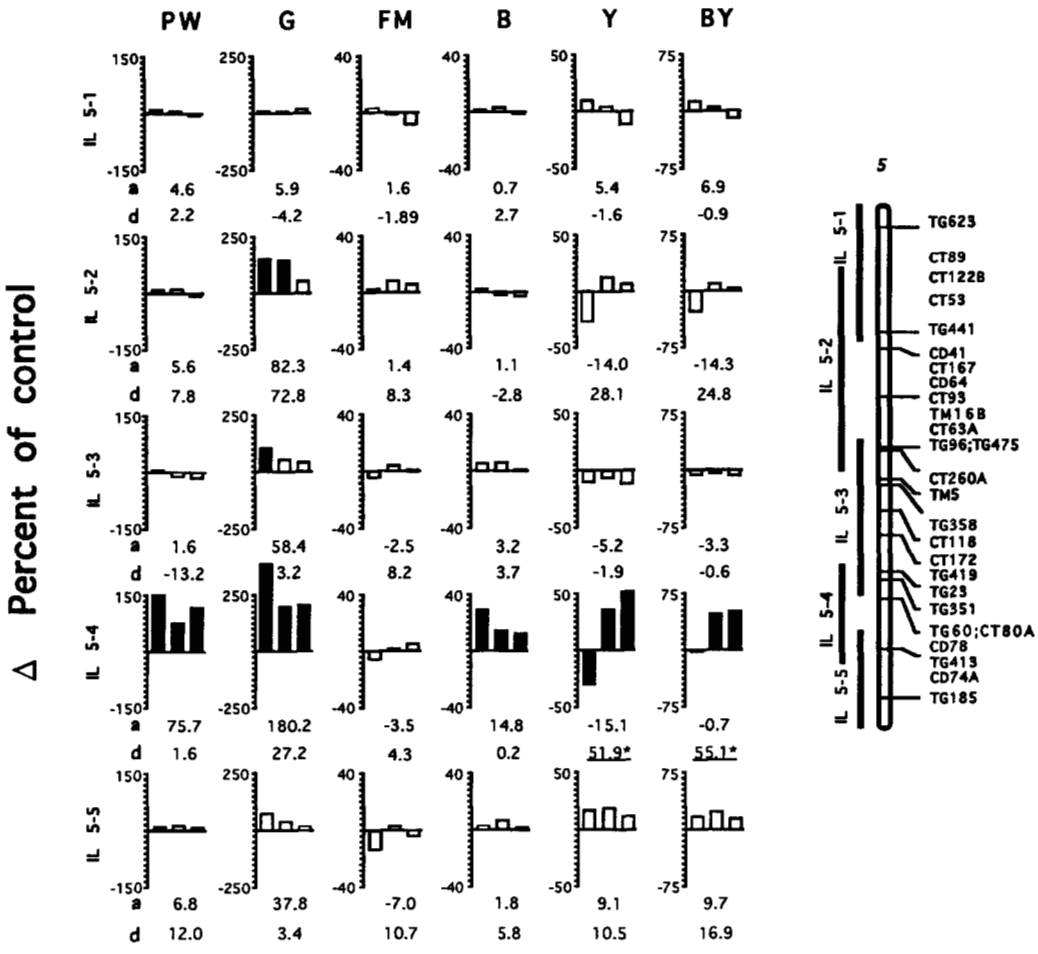


FIGURE 1.—*Continued*

was the only line for which the heterozygous was inferior to the control. At least 14 QTL were detected for BY, and the degree of dominance for this trait was the highest ($d/[a] = 10.26$) (Table 2) of all the measured traits.

**Fine mapping of QTL:** *Fine mapping of a FM QTL (chromosome 2):* In the 1993 experiment, IL2-5 and IL2-6 showed a considerable reduction (40–60%) in FM relative to the control; this effect was attributed to a single QTL that is overlapped by the two introgressions (Figure 1). To achieve finer mapping of this QTL in 1994, we conducted RFLP analysis in second and third generation progenies of IL2-5 and IL2-6 crosses with M82; 12 lines with different subsets of introgressed region were evaluated for FM (Figure 2). The effect of the entire introgression of IL2-5$^{p}$ was similar to that in the 1993 experiment (65% reduction), while its true isogenic line IL2-5$^{e}$ (plants from $F_2$ of IL2-5 × M82, selected for the cultivated tomato genotype) was not different from the control M82.

The IL2-5, IL2-6 region of *L. pennellii* appears to harbor three different QTL for FM (Figure 2). None of the recombined progenies of IL2-5 retained the magnitude of its effect on FM reduction. Two lines, IL2-5-2 and IL2-5-3, had similar effects on FM (28 and 30%, respectively). The region that spans *TG191* to *TG426* is shared between these lines and we therefore assigned *Fm2-1* to this interval. IL2-5-1 and IL2-5-4 contain longer segments of the *L. pennellii* chromosome, extending to *TG91* and *TG167*, respectively. These lines exhibited a 50% reduction in FM, which indicated the existence of an additional QTL close to *Fm2-1*. The finer position of this QTL, designated *Fm2-2*, could be inferred from the recombined progenies of IL2-6. IL2-6-1 had the same fruit mass as IL2-6 and IL2-5-5, while IL2-6-2 had larger fruit. Only *TG91* is shared by the first three of these lines and not by the fourth, so *Fm2-2* is tightly linked to *TG91*. The position of the third QTL, *Fm2-3*, was deduced from the regions covered by IL2-6-3 and IL2-6-4 (with 25% reduction in FM) but not by IL2-6-5 (with FM similar to the control). *Fm2-3* was placed between *TG50B* and *CT59*.

The map position of a QTL was located to an interval between flanking markers that were not introgressed to all the ILs carrying this QTL. According to the map (TANKSLEY *et al.* 1992) *Fm2-1* (*CD9C–CT75*) is defined by an interval of 3.2 cM, *Fm2-2* (*CD66–TG204*) by 3.7 cM and *Fm2-3* (*TG151–TG141a*) by 14.1 cM. Recombination frequencies detected for these intervals in the IL crosses were generally three to four times lower than

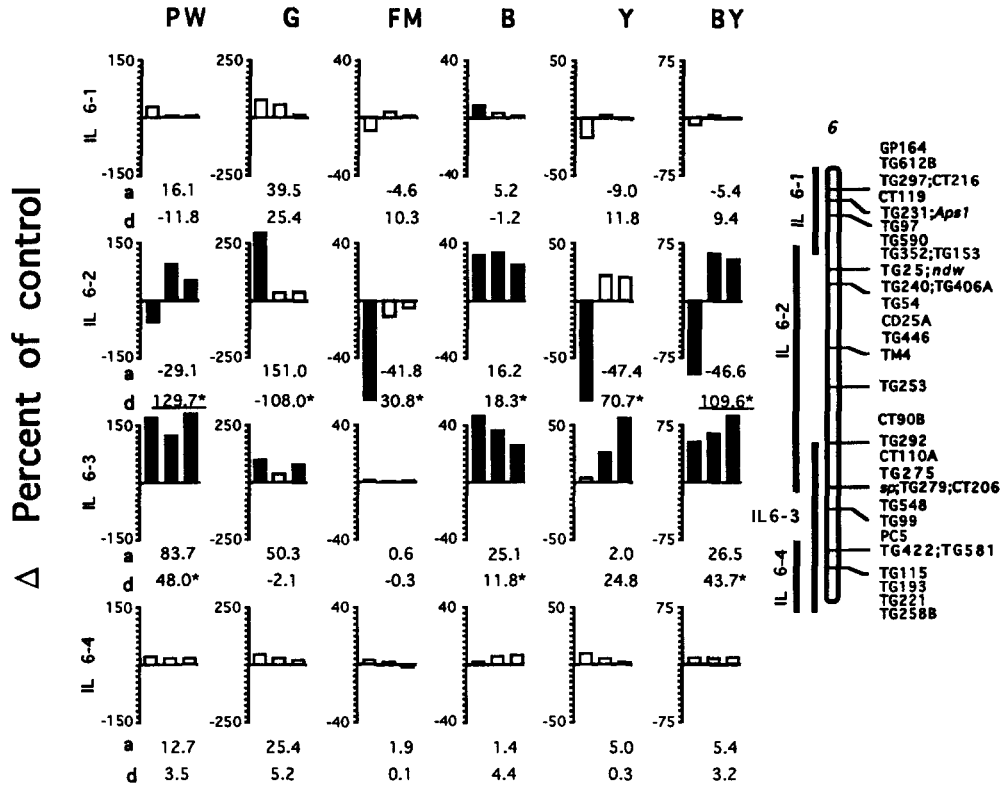


FIGURE 1.—*Continued*

those presented in the map; reduced recombination rates have been previously reported for certain *L. pennellii* introgressions (RICK 1969).

*Fine mapping of a BY QTL (chromosome 1):* In a previous study, we reported that a 37-cM introgression of chromosome *1* from *L. pennellii* (IL1-4) improved the total soluble solids yield of tomato hybrids in plots by 16% (ESHED and ZAMIR 1994a). This introgression in a heterozygous condition was effective over a 2-year period and for two genetic backgrounds. The same effect of this introgression was observed in the 1993 experiment (Figure 1). The improvement in BY was most apparent in the hybrids of IL1-4; for the fine mapping we used a similar strategy to that described above for FM but included the heterozygous lines in the analysis (Figure 3).

Seven lines derived from IL1-4 and their hybrids with M82 were measured for B and Y. Overall, the phenotypic effect of the introgressed segments on the measured quantitative traits was smaller than the effects of the FM QTL. In addition, the phenotypic variation for Y was much higher than for FM. For these reasons, the results of the finer mapping are less conclusive. The effect of the entire introgression on BY was lower than the 49% increase found in 1993 (Figure 1); the hybrid of IL1-4$^{P}$ × M82 was 31% higher than the control, while its true isogenic line, IL1-4$^{e}$, derived from the $F_2$ generation of IL1-4 but selected against the introgressed segment, was identical with M82. IL1-4 had a BY value similar to that of the control but lower than that of the heterozygous hybrid, indicating overdominance for the trait. Three derived lines, IL1-4-4, IL1-4-5 and IL1-4-6, retained their significant effects over control when tested as hybrids. All three share the introgression from *TG267* to *TG158*, which was not covered by IL1-4-7 or any of the other recombined ILs. In contrast to IL1-4$^{P}$, where the hybrid had higher BY values than those of the inbred IL and the control, the lines IL1-4-4, IL1-4-5 and IL1-4-6 had higher BY values than the hybrids and the control M82. This indicates a partially dominant mode of inheritance for the higher BY QTL in the shortened introgressions. The inconsistency in gene action between the complete and shortened segments could be explained if an additional, partially dominant QTL near *TG245* reduces BY in a homozygous condition. Indeed, IL1-4-1 and IL1-4-3 had lower BY values than the control (IL1-4$^{e}$); however, the BY value of IL1-4-2 was similar to that of the control. If such a QTL exists, it has a minor effect and should be tested in more replicates than the 10 examined here.

The conclusive result of this fine mapping attempt is that the increase in BY is associated with a 12-cM segment of *L. pennellii* between *TG53* and *TG258A*. The advantage of the different lines and their hybrids over M82 with respect to BY was an increase in either B or Y, but no consistent pattern could be observed (data not presented).

## DISCUSSION

**QTL identification using the ILs:** Of the 50 ILs tested, eight had no significant effect on any of the

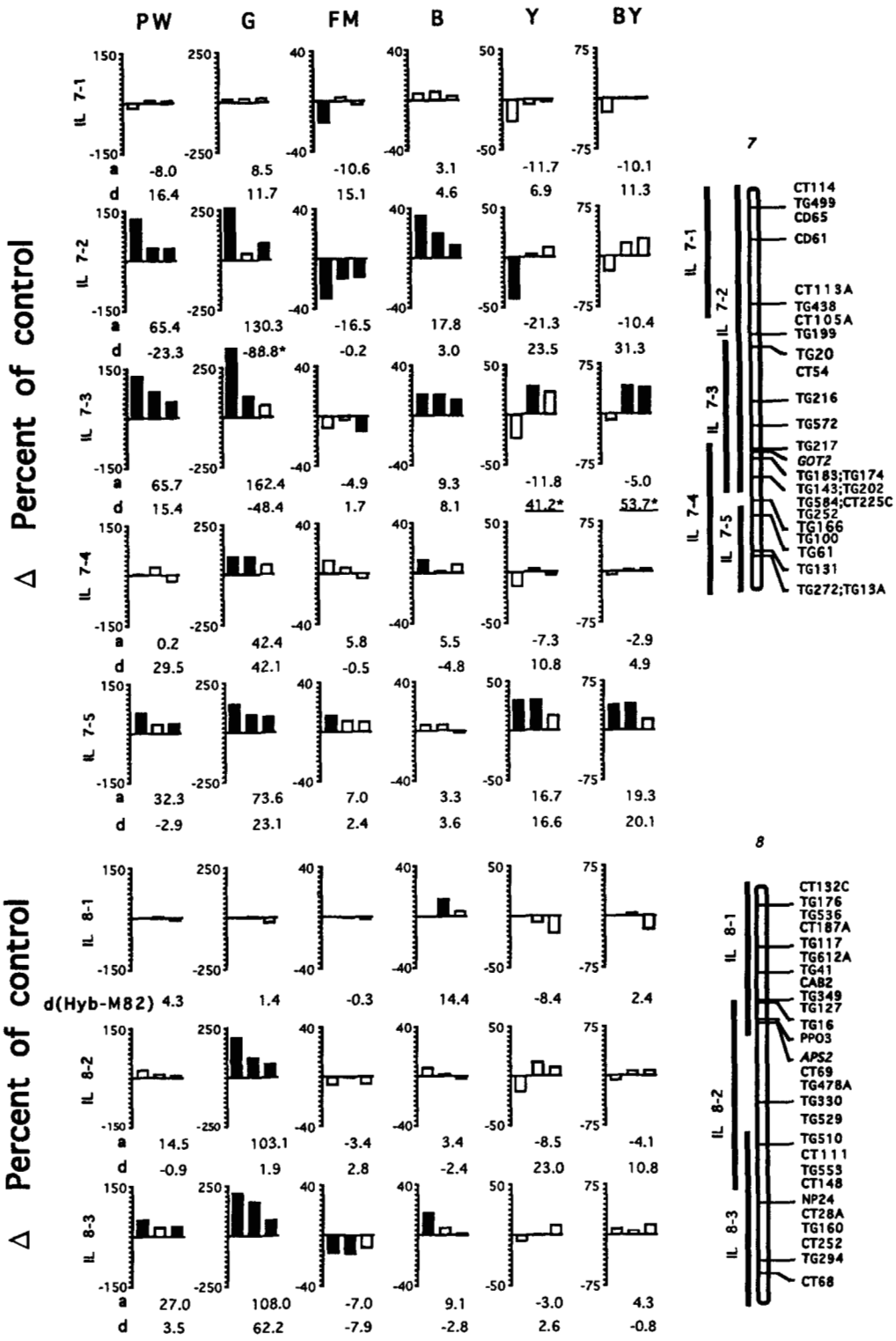


FIGURE 1.—*Continued*

traits measured. These ILs cover a total of 203 cM (17%) of the wild species genome. The 294 (49 × 6) homozygous IL × trait combinations yielded 135 that were significant at the $p < 0.05$ level. Of the 300 (50 × 6) heterozygous IL × trait combinations measured, 67 were significant at the $p < 0.05$ level in both genetic backgrounds while 36 were significant in one background only.

FM and B showed relatively low environmental variation (low CV) (Table 1) and can be compared to previous QTL findings in tomato where a similar experiment-wise error was used (5%). PW, G, Y and BY showed higher environmental variation and were assayed here in tomato for the first time using a complete linkage map. In spite of the very small number of replicates (six) used to determine the phenotypic value of each

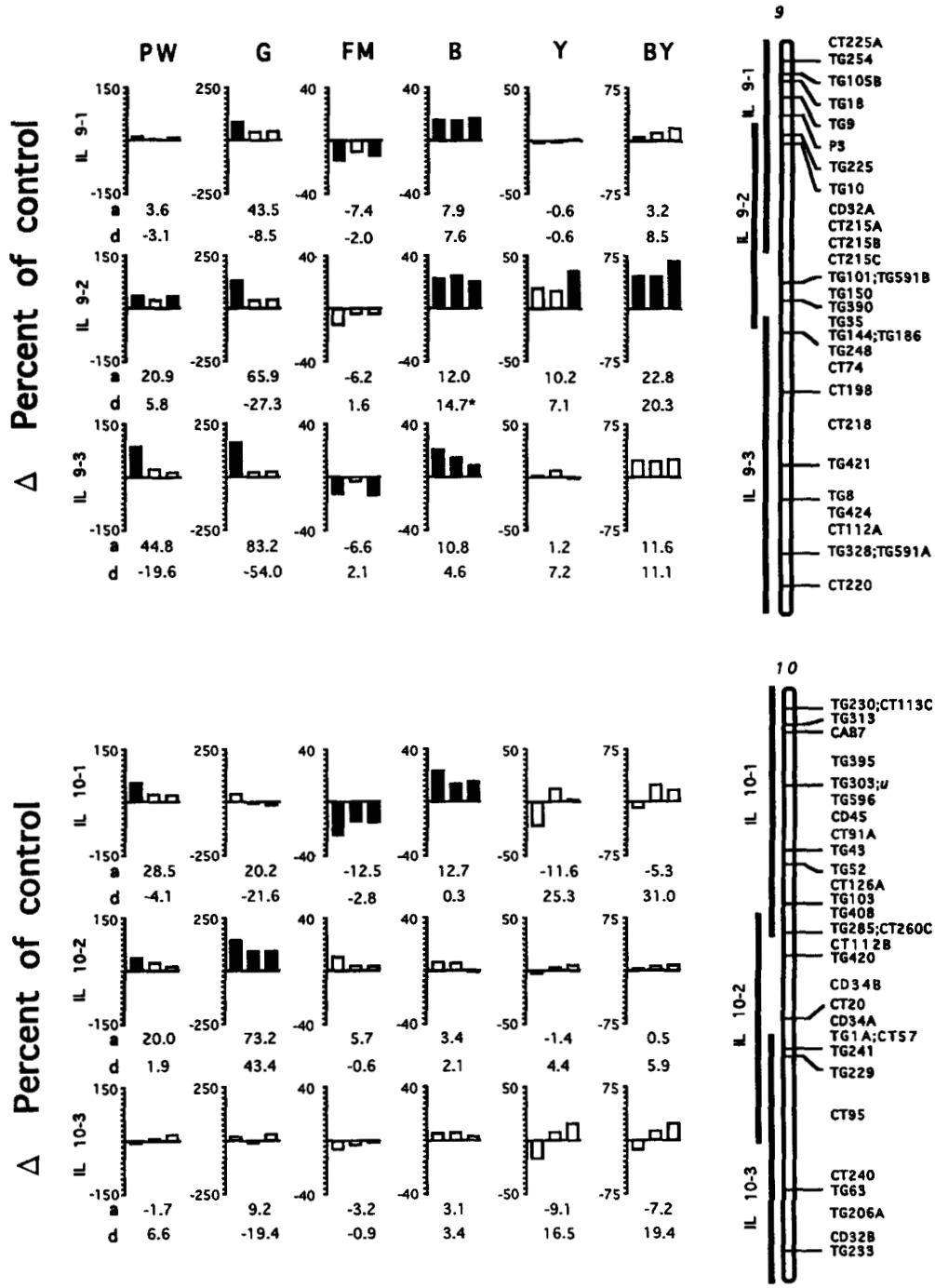


FIGURE 1.—*Continued*

IL and its hybrids, 18 QTL for FM and 23 QTL for B were identified. In previous studies of the inheritance of FM and B, using a complete linkage map in a BC1 generation derived from a cross with *L. chmielewskii,* six QTL were identified for FM and four for B (PATERSON *et al.* 1988). Mapping studies involving *L. cheesmanii* interspecific $F_2$ and $F_3$ generations revealed 13 QTL for FM and seven for B (PATERSON *et al.* 1991). In a recombinant inbred population derived from the same cross, 13 QTL were identified for FM and for B (GOLDMAN *et al.* 1995).

The advantage of the ILs in identification of QTL cannot be attributed to the phenotype of the parental lines used to generate them because the other experiments also used interspecific crosses with similar phenotypic differences between parents. One factor contributing to the high efficiency of QTL identification using the ILs is the minimal overshadowing effect. All studies of intraspecific (EMERY and MUNGER 1970) and interspecific crosses involving *L. chmielewskii, L. cheesmanii* and *L. pennellii* identified a major QTL for B on chromosome 6 linked to *sp;* the indeterminate plants always had

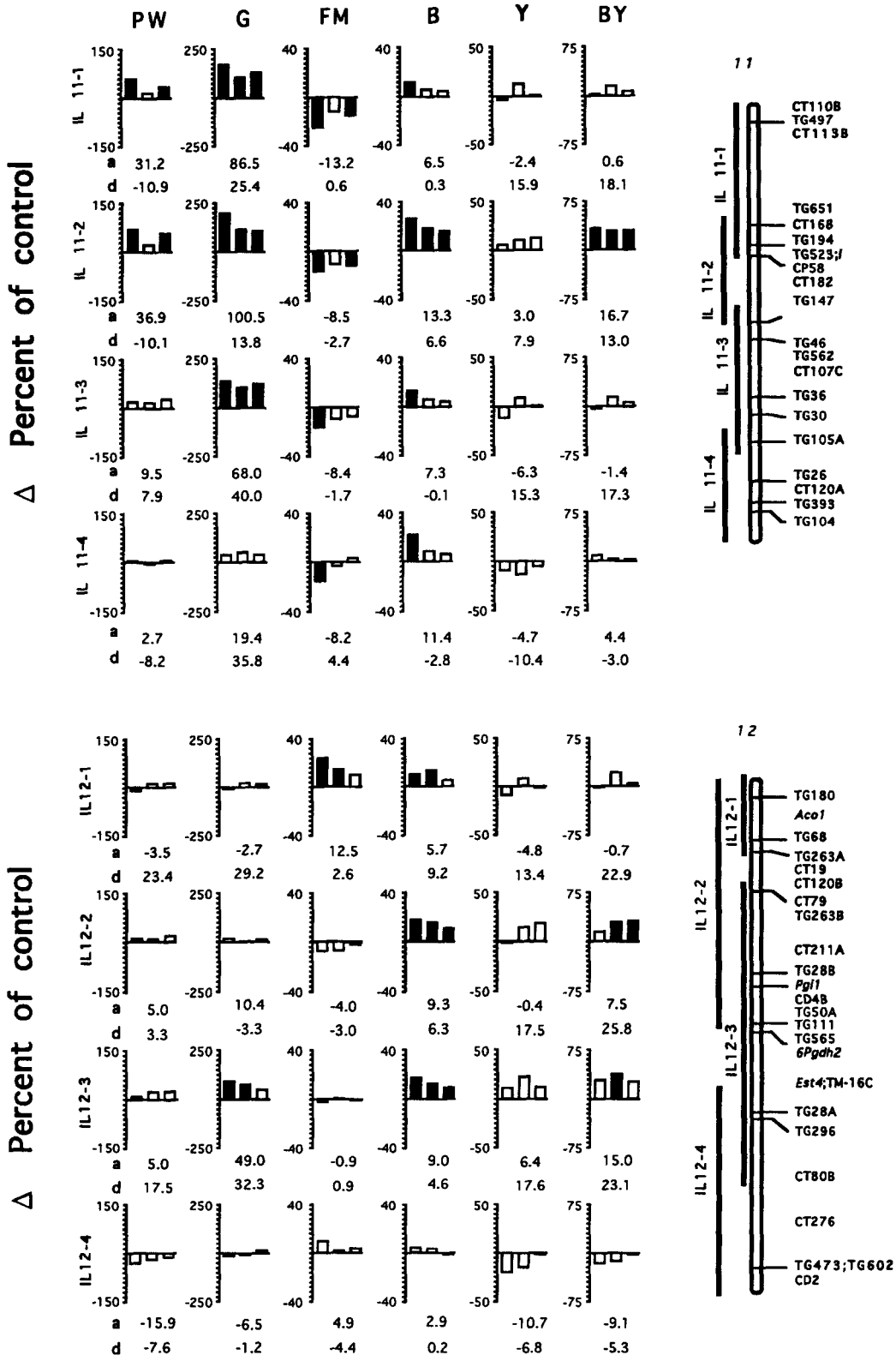


FIGURE 1.—*Continued*

higher B values. Such a gene contributes to large phenotypic variation when the effect of an unlinked marker on B is examined in a segregating population. The overshadowing effect can result from two main factors: an unequal distribution of *sp* in the subgroups of genotypes generated on the basis of the independent markers and a gene-induced elevation of the mean B value in the population. Since variation is usually correlated with the mean of a measured trait, the existance of high population means will reduce the possibility of detecting QTL

**TABLE 1**

**Mean phenotypic values for the tested genotypes**

| Genotype | No. of replicates | Plant weight (kg) | Percentage green fruit weight | Fruit mass (g) | Brix | Yield (kg) | Brix × yield (g) |
|---|---|---|---|---|---|---|---|
| *L. pennellii* | 8 | 4.4 ± 1.7 | NA | NA | NA | 0 | 0 |
| M82 × *L. pennellii* | 20 | 36.9 ± 11.2** | 74.9 ± 13.0** | 5.4 ± 0.8** | 10.3 ± 1.3** | 4.0 ± 0.7** | 415 ± 91 |
| M82 | 30 | 1.5 ± 0.5 | 3.9 ± 4.0 | 58.2 ± 7.1 | 4.3 ± 0.2 | 8.2 ± 1.7 | 361 ± 82 |
| M82 | 30 | 1.5 ± 0.5 | 3.9 ± 4.0 | 58.2 ± 7.1 | 4.3 ± 0.2 | 8.2 ± 1.7 | 361 ± 82 |
| M82 × A8 | 20 | 1.5 ± 0.3 | 3.1 ± 2.5 | 64.7 ± 8.1** | 4.7 ± 0.3* | 8.6 ± 1.5 | 396 ± 66 |
| A8 | 23 | 1.6 ± 0.5 | 6.8 ± 5.0 | 73.0 ± 8.0** | 5.0 ± 0.4** | 7.0 ± 1.6* | 351 ± 89 |
| 49 inbred ILs | 6 | 2.2 ± 0.9** | 14.4 ± 18.5** | 50.9 ± 11.0** | 4.9 ± 0.5** | 7.0 ± 2.2** | 347 ± 115 |
| M82 × 50 Ls | 6 | 1.8 ± 0.5* | 8.9 ± 6.5** | 56.0 ± 6.0 | 4.7 ± 0.4** | 8.9 ± 1.2 | 424 ± 76** |
| A8 × 50 ILs | 6 | 1.9 ± 0.6** | 7.4 ± 5.3** | 60.7 ± 6.8* | 4.9 ± 0.4* | 9.2 ± 1.4 | 461 ± 96** |
| C.V.[a] | | 25.3 | 32.5[b] | 11.5 | 6.9 | 21.2 | 22.2 |

Mean phenotypic values and standard deviations of three genotypic groups are presented. The genotypic groups are as follows: the parental species, *L. pennellii, L. esculentum* (cv M82) and their interspecific hybrid; the *L. esculentum* inbred lines M82, A8 and their hybrid; the homozygous introgression lines (ILs) and their hybrids with M82 and A8. All means were compared to M82 except for A8 × 50 ILs that were compared to M82 × A8. Means marked with *, ** differ significantly (*t* test: $p < 0.05$, $p < 0.01$ respectively). NA, data not available because the plants did not set fruit.

[a] Coefficient of variation (%) was calculated on the basis of all genotypes.

[b] Coefficient of variation (%) was calculated after a square root transformation.

with milder effects. An additional factor that might account for the large number of QTL detected in this study is the exposure of novel variation not detected in conventional segregating populations. The two examples of such variation are the male gamete eliminator (IL8-1) and the *ndw* mutation (IL 6-2). These genes have not been previously reported for any of the $F_2$-segregating populations of *L. esculentum* × *L. pennellii,* although this cross was used extensively in genetic studies. Only when introgressed into the cultivated background, without additional wild species chromosome segments, were these genes identified (WEIDE *et al.* 1993). Such an inheritance pattern is probably due to other unlinked epistatic genes from *L. pennellii.* The same mode of inheritance can account for QTL and may be an important source of trangressive variation.

The QTL for PW and G had the largest effects of all the traits measured. These parameters allowed the identification of 16 and 22 QTL, respectively, despite the large environmental variation. Yield is among the most difficult traits to manipulate genetically; not only does every metabolic pathway ultimately affect reproduction, but the environment is also a major determinant of yield. Genetic analysis of yield in interspecific crosses is often affected by some overshadowing QTL associated with partial sterility. In this study we identified at least four such QTL, in which homozygosity for the wild species allele resulted in almost complete steril-

**TABLE 2**

**The number of significant effects ($p < 0.05$) of *L. pennellii* introgressions on the components of genetic variation for the quantitative traits studied**

| Genetic components[a] | Plant weight | % Green fruit weight | Fruit mass | Brix (TSS) | Total fruit yield | Brix × yield |
|---|---|---|---|---|---|---|
| a+ | 22 | 33 | 2 | 31 | 1 | 5 |
| a− | 2 | 2 | 20 | 1 | 9 | 7 |
| d+ | 2 | 0 | 0 | 3 | 7 | 8 |
| d− | 0 | 2 | 0 | 0 | 0 | 0 |
| od | 1 | 0 | 0 | 0 | 2 | 5 |
| Mean $d/[a]$[b] | 0.06 | 0.06 | 0.34 | 0.45 | 2.16 | 10.26 |
| Minimal number of QTL[c] | 16 | 22 | 18 | 23 | 11 | 14 |

[a] The genetic components of the variations are as follows: additive (a), dominance deviation (d), and overdominance (od). Values higher relative to the control genotype are indicated by + the values lower than the control are indicated by −.

[b] The degree of dominance (mean $d/[a]$) was calculated on the basis of all ILs, regardless of significance of *d* and *a*.

[c] The minimal number of significant QTL affecting a trait was calculated on the basis of the assumptions described in MATERIALS AND METHODS.

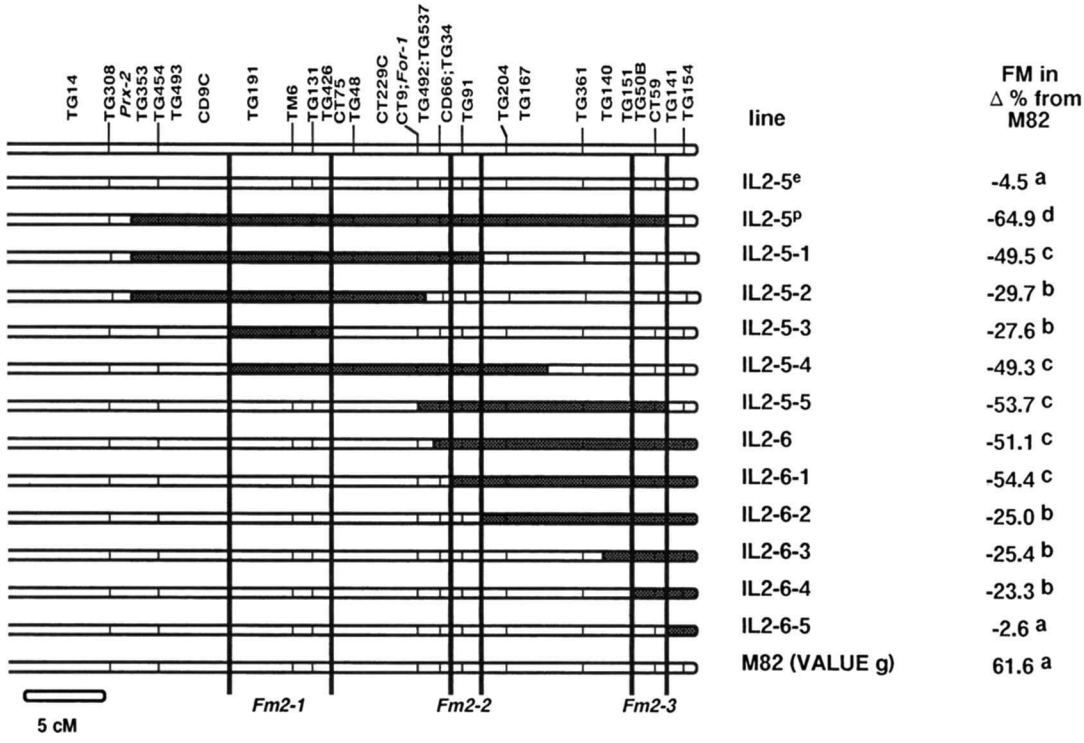


FIGURE 2.—Fine mapping of QTL for fruit mass (FM) on the distal end of the long arm of chromosome 2. The only *L. pennellii* chromosome segments introgressed into the listed lines are marked by the dark bars. ILs 2-5$^{p}$ and 2-5$^{e}$ are truly isogenic and are derived from an $F_2$ of IL2-5 crossed to M82 and selected by RFLPs to be homozygous for the *L. pennellii* alleles ($^{p}$) or the cultivated tomato alleles ($^{e}$). For each line, the phenotypic value (presented as percentage difference from M82, Δ%) based on 10 replications was determined for the homozygous recombined ILs. Multiple range test by "Each pair comparison" with an alpha level of 0.05 was performed between the lines; different letters denote significant differences. The smallest chromosome segment that retains a significant effect on FM relative to the isogenic lines is marked by two vertical lines and is the postulated position of the FM QTL (*Fm*).

ity (on chromosomes *1, 3, 6* and *7*). If we exclude IL6-2 (because it carries *ndw*), the remaining three QTL can account for partial sterility in >50% of the plants of the $F_2$ generation [$1 - (3/4)^3$]. The IL population revealed at least 11 significant QTL for yield, of which seven *L. pennellii* segments were associated with increased yield. The effect of selected chromosome segments from *L. pennellii* has been previously reported (DE VICENTE and TANKSLEY 1993; ESHED and ZAMIR 1994a); as in the present study, introgressed regions near the centromeres of chromosomes *1* and *7* and from the long arms of chromosomes *1* and *5* were significantly associated with increased yield.

**Gene action of detected QTL:** The gene action of detected QTL was determined by comparing the homozygous IL to its hybrid in the same genetic background. The inheritance modes of the QTL for FM and for B are intermediate between additivity and dominance, in agreement with PATERSON *et al.* (1991b). High deviations from the general additivity can be found when other genes with strong pleiotropic effects are involved, such as the poor performance of IL6-2 (*ndw*) leading to the large dominance deviation for all measured traits.

In contrast to the strong heterosis for PW of the interspecific $F_1$ hybrid (Table 1), the QTL for PW showed additive inheritance. General additivity was also detected for G. However, effects contrary to expectations based on parental line phenotype were seen for IL2-1, which had small plants and early fruit set. In contrast to the other measured traits, Y was strongly associated with overdominance. Significant dominant deviation for yield was detected in seven of the ILs and was always associated with increased yield. A similar pattern of results was obtained in an experiment designed to identify QTL for yield in an intraspecific cross between two elite inbreds of maize (STUBER *et al.* 1992).

The most striking feature of the interspecific hybrid was its vigor for PW (Table 1). Dissection of the wild genome into small independent fragments revealed that only the indeterminate lines, IL6-2 and IL6-3, exhibited positive dominance deviation for PW; these lines can explain only a small fraction of the heterotic effects found for this trait in the interspecific hybrid. On the other hand, at least four QTL with heterotic effects for BY were identified. No heterotic effect for this trait was observed in the interspecific hybrid. We therefore suggest that by elimination of the factors responsible for the low productivity of the $F_1$ hybrid, the vegetative vigor was transformed into a reproductive one.

In 1993 DE VICENTE and TANKSLEY reported on trans-

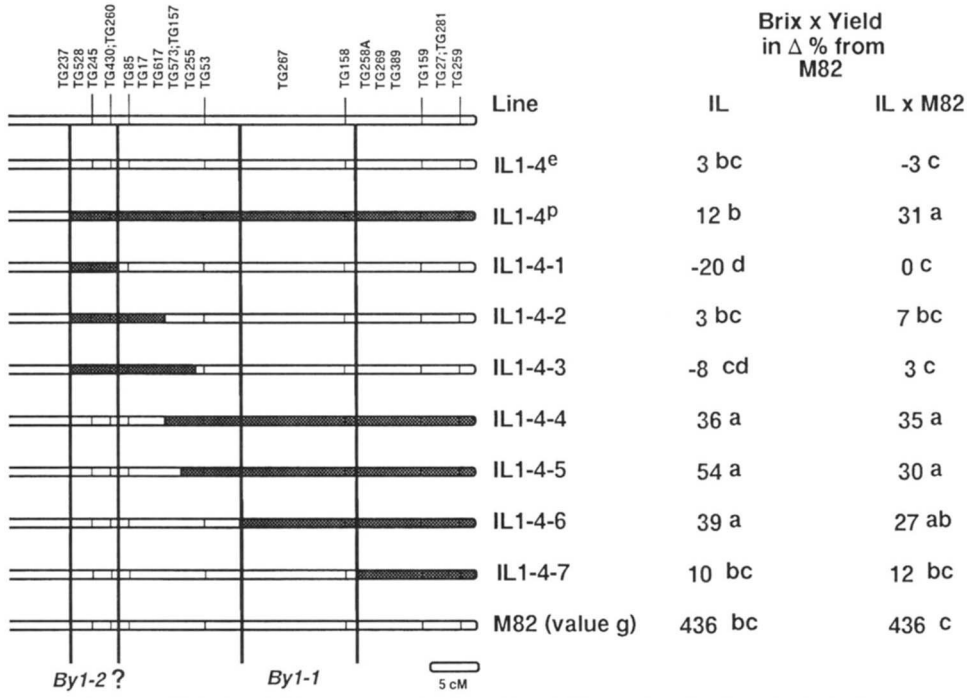


FIGURE 3.—Fine mapping of QTL for yield of total soluble solids (BY) in the distal end of the long arm of chromosome *1*. The only *L. pennellii* chromosome segments introgressed into the listed lines are marked by the dark bars (all lines are progenies of IL 1-4). ILs 1-4$^{p}$ and 1-4$^{e}$ are truly isogenic and are derived from $F_2$ of IL 1-4 crossed to M82 and selected by RFLPs to be homozygous for the *L. pennellii* alleles ($^{p}$) or the cultivated tomato alleles ($^{e}$). For each line, the phenotypic value (presented as percent difference from M82, $\Delta\%$) based on 10 replications was determined for both the homozygous ILs and the heterozygous IL × M82. Multiple range test by "Each pair comparison" with an alpha level of 0.05 was performed between the inbreds and between the hybrids separately; different letters denote significant differences. The location of the QTL is determined by the smallest chromosomal segment that retains a significant effect on BY and is marked by the area between the vertical lines, which is the postulated location of the QTL for this trait.

gressive segregation in 10 out of 11 quantitative traits measured on $F_2$ seedlings of the same interspecific cross. In this study we show that the same is true for quantitative traits measured on mature plants and for traits having economic importance.

**Sensitivity of QTL to genetic background:** Cultivated tomato varieties represent only a small fraction of the variation presented in Lycopersicon (RICK 1982; MILLER and TANKSLEY 1990). This leads to the expectation that significant effects of the introgressions found in one cultivar are likely to be maintained in others. In this study, the effect of the *L. pennellii* introgressions was tested using an additional processing inbred line (A8) with larger FM and higher B. None of the 300 possible interactions with genetic background was significant. These results confirm the broad and dramatic effects of the novel variation introduced into the cultivated crop.

**Fine mapping of QTL:** To overcome the problem of high resolution mapping of QTL in conventional crosses, PATERSON *et al.* (1990) used selected overlapping recombinant chromosomes. In this study we demonstrate that a FM QTL can be resolved into three linked QTL; it is possible that upon finer mapping additional loci will be revealed. *Fm2-1* was mapped to an interval of 3.2 cM (Figure 2), which in certain areas of the tomato genome can be covered by a single YAC (SEGAL *et al.* 1992).

The heterotic effect of the 37-cM introgression of IL1-4 on BY was consistent over 3 years and for different genetic backgrounds and growing stands (ESHED and ZAMIR 1994a). Finer mapping of this BY QTL suggested that two loci were involved: a partially dominant gene originating from the wild parent was responsible for the increase in BY and a linked recessive gene of *L. pennellii* origin reduced BY. It appears that combined action of these QTL, which fits the pseudo-overdominance model for heterosis (CROW 1952), resulted in the lower BY of the homozygous IL1-4 compared to its hybrids.

**Implications for general genetics and plant breeding:** For each of the traits analyzed in this study, introgressions with phenotypic effects of different magnitudes were identified (Figure 1). These results are in agreement with the accumulated data from numerous QTL studies that establish definitively that polygenes vary widely in their effects, and in many instances a large proportion of the variation can be explained by the segregation of a few major QTL (TANKSLEY 1993).

Although the number of replicates used in the study was very small (six per genotype), more QTL could be identified by comparison with similar studies in tomato, where each genotype has been measured from a few

dozen to a few hundred times. The numbers of QTL reported in this study are skewed downward for the following reasons. First, it is not necessarily correct that two overlapping introgressions with a similar effect carry the same QTL. Second, an IL can carry more than one QTL, as demonstrated here for IL2-5 and IL2-6. The higher sensitivity of this population is a result of the minimal genetic variation within the lines.

A statistical advantage for the experimental design is the use of a common control for all lines that can be grown in large numbers and can ensure enough degrees of freedom. An additional advantage of the ILs is the ease of distinction between additive and dominance effects. Moreover, once an inbred IL is produced, its effect can be determined for various genetic backgrounds (only in a heterozygous state) and in different environments. This factor is of major importance for identification of QTL with broad effects.

We favor the development of a permanent resource of ILs that provides several advantages over conventional populations. In addition to the high efficiency of QTL identification and fine mapping, it could also contribute to investigations of interaction between QTL. Reliable estimates of the interaction between QTL are difficult to obtain in segregating populations since the frequencies of some of the genotypic combinations are too low to allow meaningful statistical comparisons. The availability of nearly isogenic lines containing different QTL would allow examination of these lines in various genotypic constitutions in balanced experiments aimed at the precise analysis of epistatic interaction.

An important advantage of the IL approach is its immediate applicability in breeding. If the recipient genome is a leading variety, the derived lines may represent a significant improvement and a basis for the introduction of a new cultivar. ILs can also be applied in a number of ways other than those described in this article (ESHED and ZAMIR 1994b), such as mapping of new DNA clones to the genome, identification of region-specific DNA markers, and fine mapping of qualitative genes.

The main disadvantage of IL populations is the long time and the large amount of work required for their development. We estimate that after complete genotyping of a BC1 population and selection of the appropriate lines providing coverage of the genome with minimal overlaps, two additional cycles of backcrosses accompanied by genotypic and phenotypic selection are required. In a selfed BC3 population the founders of an IL population can be identified. It is however expected that in outcrossing species the proportion of genes associated with deleterious recessive mutations would be higher than reported here.

Wild species represent a widely divergent gene pool for the improvement of cultivated plants. Exotic germplasm have been used extensively for breeding for simply inherited traits such as disease resistances. Although in a pioneering study RICK (1974) has demonstrated that high soluble solids content in tomato could be improved through wild species crosses, the use of these resources for improvement of complex traits was considered largely impractical because of the many undesirable traits carried by wild species. This study demonstrates that genes from a very small green-fruited, poor-yielding wild species can serve as a source for many agriculturally important traits. Even traits that were not apparent in the parental lines eventually segregated among the ILs.

Methodologies for the identification and mapping of genes underlying quantitative traits in plants have advanced considerably in recent years since the advent of marker-saturated linkage maps (TANKSLEY 1993). The developments in marker technologies have not however been accompanied by corresponding progress in population structures. In this study we describe a new population capable of facilitating the utilization of wild germplasm by providing the means for identification and fine mapping of QTL.

All DNA clones were provided by Dr. S. D. TANKSLEY, except for TM clones provided by Dr. E. LIFSCHITZ and GP clones provided by Dr. C. GEBHARDT. We thank G. GERA from Akko Experiment Station for his assistance in conducting the field trials and T. PLEBAN, H. VAN OSS, T. BLOCH, M. EMANUEL and A. NATOR for technical assistance. We thank Dr. S. D. TANKSLEY, Dr. I. PARAN, Dr. H. VOET and N. ORI for stimulating discussions and S. SMITH for editing. This research was supported in part by grant no. US-2427-94 from BARD, The United States-Israel Binational Research and Development Fund. Seeds of the ILs have been distributed through the Tomato Genetics Resource Center, University of California, Davis. The IL database has been deposited in the Solanaceae database and is available through the internet: jcn5@nightshade.cit.cornell.edu.

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Communicating editor: M. R. HANSON